Stopover ecology of autumn-migrating Bluethroats (*Luscinia svecica*) in a highly anthropogenic river basin

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Summary

Wetlands are highly productive habitats used by many avian species as stopover sites during their migrations. However, these habitats are highly threatened by anthropogenic activities, such as land use changes, the introduction of exotic species and global warming. Further understanding on the spatiotemporal use of wetlands and their surrounding areas by migrating birds is essential to predict how these changes might affect avian *en route* ecology. We selected a habitat-generalist passerine, the Bluethroat *Luscinia svecica*, as model of how migratory birds exploit a highly anthropogenic river basin in southwestern France (i.e. Barthes de la Nive) during autumn migration. We captured and radiotracked 29 young Bluethroats in this region to shed light on different aspects of their stopover ecology and behaviour, such as stopover duration, habitat selection and home range size. We also characterized Bluethroat diet and arthropod availability in different habitats. Bluethroats positively selected pure or mixed reedbeds (associated with sedge), hydrophilous tall grasslands and corn crops. Birds staying more than just one day 8.4 days on average, used preferably corn crops. Home range sizes were on average 5.8 ha (fixed kernels K95) and high occupancy area (K50) was 1.36 ha with large individual variation. Bluethroats stopping over with low fuel loads tended to have larger home ranges and used preferentially corn crops, wet or mesotrophic grasslands and rural paths. Reedbeds were typically used as roosting habitat for the majority of birds, being on average 397 m apart from their daytime core areas. Short-staying birds tended to show higher fuel loads and restricted their activities to a smaller home range (1 ha) in pure and mixed reedbeds. The diet of Bluethroats was dominated by ants, spiders and beetles that were particularly abundant in corn crops. The use of corn crops by autumn-migrating Bluethroats in our study site seems a reasonable solution in a highly altered environment. Reducing the use of insecticides in these crops and delaying the harvesting time after mid-October are two supplemental measures that, together with a good management of the remaining wetland patches, could greatly favour Bluethroats and other migratory species in this region.

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Ethics statement: All data and information from external sources used for the analyses and preparation of the manuscript are properly cited. The conclusions are entirely based on our own results. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Introduction

The global conservation of migratory birds not only relies on the protection of their breeding and wintering habitats, but also on the presence of suitable stopover sites along their migratory routes (Hutto 2000, Yong 1998 Newton 2008). Coastal marshes, estuaries and other types of wetlands are highly productive habitats largely used during migration by waterbirds and other avian species, constituting key conservation areas (Czech and Parsons 2002). Wetland habitats experienced a dramatic reduction and an increased fragmentation during the 20th century, mainly as a consequence of the pressure of human activities, such as urbanization and the drainage for agricultural use (von Behren 2007; Whited et al 2000; Czech and Parsons 2002). As a result, wetlands usually remain now embedded in a complex and highly-altered human matrix, where every year migrating birds rest and search for food to undertake their next flight bout.

The wetland remnants that many birds use as stopover sites are normally small and face some common problems that, in some cases, can be mitigated by human intervention. For example, many wetland managers implement measures to avoid clogging, which could lead to bush encroachment and the progressive disappearance of marsh vegetation (Clark and Wilson 2001). The control of invasive and exotic species, that can alter wetland biodiversity and functioning, is also a common practice (Fontanilles et al. 2014; Arizaga et al. 2013). These measures would increase the quality and carrying capacity of the wetlands, which would be very beneficial for migrating birds (e.g. fuel deposition; Delingat and Dierschke 2000). Another aspect that has hitherto received little attention is the potential management and planning of the areas surrounding the wetland. These adjacent areas might be intensively used by migrants given the restricted size of wetland patches and the potential high intra and interspecifc competition with other migratory and resident individual birds. This situation could be particularly exacerbated during the migration peaks, when large number of individuals can co-occur in a single location (Newton, 2004). Such circumstance predicts that many migrants will be forced to expand their home-ranges and use alternative habitats out of the wetland. In this context, identifying which alternative habitats are positively selected by migrating birds during their brief stopovers would be essential to design buffer areas that best meet the requirements for these migrants *en route*. However, this knowledge is limited in many key stopover areas..

In this study, we analysed the stopover ecology of migrating Bluethroats *Luscinia svecica* in Barthes de la Nive (France) during autumn migration. Barthes de la Nive is a mosaic of wetlands, riparian woodlands and farmlands located near the Adour River mouth in the Southwestern Atlantic coast of France. The scattered wetlands in this region attract a large diversity of both aquatic and non-aquatic birds during migration periods (Fontanilles et al. 2011). The only radiotracking study carried out in this area so far showed that the globally endangered Aquatic Warbler *Acrocephalus paludicola* had a strong preference for reedbeds but, to a lesser extent, it also made use of some farmlands (Fontanilles et al. 2014). This highlights the relevance that the surrounding matrix might have even for a wetland specialist as the Aquatic Warbler. Conversely, Bluethroats are migratory birds that can use a large range of habitats, mainly reedbeds and marshlands (Arizaga et al. 2006; Musseau et al. 2017), but also bushlands, woodland and farming habitats (Cramp 1988; Cornulier et al. 1997; Chiron, 2017, Berndt and Hölzel 2012), making it an interesting model to study its stopover ecology and habitat selection during migration. Arizaga et al. (2011) radiotracked 20 autumn-migrating Bluethroats in Txingudi (North Spain), a wetland located less than 30km away from Barthes de la Nive. Their results showed a strong selection for reedbeds, low-halophytic vegetation and tidal flats. However, Txingudi is located in a more urbanized environment that probably restricts bird movements, and its proximity to the river mouth allows the presence of habitats that are lacking in Barthes de la Nive (e.g. halophytic vegetation). On the other hand, bird ringing information obtained for both wetlands during autumn migration showed dramatic differences in the number of within-season recoveries, which are much more usual in Txingudi than in Barthes de la Nive (Arizaga et al. 2011; Fontanilles unpublished data). These differences could be a consequence of a longer stopover duration of Bluethroats in Txingudi than in Barthes de la Nive, but they could also be caused by the existence of larger home ranges in Barthes de la Nive, something that would be possible in its much less urbanized surrounding. All these aspects suggest a different stopover ecology and behaviour of Bluethroats between both wetlands in spite of their geographic proximity that remains still unresolved.

In order to better understand the stopover ecology of the Bluethroat in Barthes de la Nive, we performed a radiotracking study during autumn migration that aims to shed light on (1) the stopover duration and the proximate factors that affect it, (2) habitat selection and home range sizes, and (3) we complemented the study with an analysis of Bluethroat diet and the availability of food resources. Although Bluethroats are not globally threatened, some populations have been considered to be under high risk of extinction (Huntley et al. 2007). Consequently, we expect that the spatial information generated in this study could be valuable for the competent authorities to design management practices contributing to the conservation of Bluethroats and other birds during their migrations.

MATERIALS AND METHODS

Study area and vegetation map

Barthes de la Nive (43°27'N; 01°28'W) is a 442-ha mosaic of natural and anthropogenic habitats (Fig. A1), whose remaining wetlands have been maintained safe from complete drainage due to its role in reducing the risk of flooding in Bayonne city. The wetlands are connected to the Adour river by channels, so that its hydrology is influenced by the flow of the river and the tidal regimes. However, its natural influence and ecologic functions in Adour estuary were drastically affected to urbanize the city, to develop port facilities and dykes, which virtually destroyed the original mudflats and intertidal areas. Our study site is now a protected area included in the European Natura 2000 network (FR7200786). The non-urban areas near the river have been widely used for pasture, as hay meadows and other agricultural purposes, being corn plantations the primary crop nowadays. Farming in the region uses a reasonably low quantity of fertilizers and no insecticide. Field abandonment and lack of management is increasing gradually bush and tree encroachment, which is changing dramatically the landscape. A vegetation map was obtained from photo-interpretation and field validation for summer 2014 and 2015 (see Fig. A1 in Suplementary Material, Table1). This approach showed the relative importance of each habitat in the region (see Table 1).

Bluethroat trapping and body measurements

Mist-netting sessions were performed from mid-August to late September when migrating Bluethroats stop over in this region during their post-breeding migratory period. Note that Bluethroats do not breed in Barthes de la Nive or use it for moulting (Fontanilles et al. 2011). Ringing sessions took place in five different locations across the study area: four wetlands and one corn crop (see details in Supplementary Material Fig. A1, Ap. 3, Table 2). These five sites were reasonably distant to each other (see Fig. A1) to reduce potential geographic bias and, according to previous studies (Fontanilles et al. 2011, Fontanilles 2014), they represent the two main habitats (i.e. reedbed, corn crops) where Bluethroats occur during their stopover at Barthes de la Nive.

To maximize the number of captures, we used one male song playback from 30 minutes before dawn (when mist-nets were open) until a tagged bird was released (when mist-nets were furled; de la Hera et al. 2017). By using the tape lures only 30 minutes before sunrise, we reduced the possibilities of forcing the landing of migrating Bluethroats and we expected to capture only birds that decided voluntarily to stop over in our study area (Schaub 1999; Arizaga et al. 2015). During our ringing sessions, we captured 58 Bluethroats (28 in 2014 and 30 in 2015).

Several morphological measurements were taken from each bird in order to obtain a composite index of bird body size (Freeman and Jackson 1990, Tellería et al. 2013, see Supplementary Material). We also recorded body mass (±0.1 g) and standard scores of fat and muscle (Busse 2000). Body size-corrected measurements of body mass were used to estimate individual fuel loads. This was done using a linear regression of body mass on body size (see Supplementary Material Ap. 2, Fig. A2), where individuals with higher fuel loads showed more positive residuals (Salewski et al. 2009).

Radio tracking information

Out of the 58 Bluethroats captured, 29 juveniles were equipped with a radio-transmitter, with a minimum of 4 radiotagged individuals in each of the 5 ringing sites (25 birds were trapped in the reedbeds and 4 in the corn crops; see details in Supplementary Material, Ap. 3, Table A2). Life expectancy of the emitters is typically more than 17 days and the average detection distance is 80-300 meters. We only tagged first-year birds because the study site is mainly used by this age group, and because juveniles face their first autumn migration and, consequently, their habitat choice cannot be influenced by previous experience (Piper 2011).

On the day of capture, monitoring of tagged Bluethroats started at least one hour after the bird was released in order to avoid bias linked to potential stress behaviour. For birds that stayed in the area the following days after capture (see below), they were normally monitored 8h per day during, normally, 3-4 days in long-staying individuals. After this period, we checked their presence every day, but the intensity of the radiotracking typically got reduced and depended on other duties associated with the project, particularly, the trapping and monitoring of other individuals (see Supplementary Material Ap.3 for more details).

The positions of the birds were obtained normally by triangulation (3 vectors taken consecutively within less than 10 minutes), but we used bi-angulation in those cases in which landscape barriers (like canals, rivers or dense vegetation) impeded taking more than two informative vectors, or just one vector plus an estimation of the actual distance to the bird when this was observed. We used Sika receivers (Biotrack Ltd) and Yagi antennas to find the birds, and vectors were delimited using a GPS (to determine observer position; Garmin Ltd.) and a compass (to obtain magnetic Azimuth). All this information was computerized using the software Cartoexploreur (Bayo Ltd.), and we considered the centroid of the triangle determined by the three corresponding vectors as the most likely geographic position of the bird, or the intersections between lines when

two vectors were only available. Prior to the start of radiotracking, observers were trained in the study area and the accuracy of the triangulation method was assessed. The average error found in the estimation of the positions of transmitters hidden in the study area was 14.5±1 m (n=69), which can be considered enough given the purpose of studying main habitat selection.

Stopover duration and its determinants

We used the number of days spent by each Bluethroat after being tagged (assessed by the radiotracking survey) as a proxy of stopover duration. This approach is expected to provide a better idea than ringing recaptures on how long Bluethroats stopover in Barthes de la Nive, since ring-recovery data are spatially restricted, have a lower detection probability and strongly depend on a good sampling strategy (Chernetsov 2012). According to the non-Gaussian distribution of stopover durations (see Fig. A3), we performed non parametric tests (Wilcoxon tests, Kruskal-Wallis tests and Spearman correlations) to evaluate which factors (year, sex, site, date of capture, muscle development, fat accumulation and body condition) better correlated with the observed variation in stopover duration.

Habitat selection

Initially, we tested whether Bluethroat locations were randomly distributed across habitats. We applied the quadrats method (Zaminetti 2005) by defining a grid of K squares 100 x 100 m enveloping all the radio-tracking points. The theoretical distribution K_{th} (n) was obtained following the Poisson's law: $K_{nth}= [K*(D^n/n!)]*\exp(-D)$ where n is the number of points per mesh, K(n) the number of stitches having n points, N is the total number of locations and D is the average density of locations by cell that is defined as N divided by K. The existence of significant differences between the two distributions (i.e. K (n) and K_{th} (n)) was assessed using a Kolmogorov-Smirnov test.

Secondly, for assessing habitat selection, we calculated for each habitat the electivity index of Jacobs (1974) I_h = U - D / (U + D -2U*D) where U is the proportion of locations in habitat h and D the proportion of this habitat in the study area. The index ranges between -1 (strong rejection of a particular habitat) and 1 (strong selection). We used the proportion of locations instead of the proportion of areas in core areas to take into account the edge effects and to be more precise with the actual habitat used. We excluded habitats poorly represented showing less than 5 locations.

Home range estimates

The overall home range size of each individual Bluethroat was estimated by the model of 95% kernel (K95; Worton 1989). The K95 approach is usually used in this type of studies, which would allow between study comparisons (Börger *et al.* 2006). Areas of high occupancy were also estimated using the 50% kernel (K50), considered as a good estimator of core areas (Börger et *al*. 2006). We calculated the overall home range with all the locations for each bird and also for each day when there was a minimum of 10 positions. Home range sizes were processed using the Ranges 8v2.10 software (Anatrack ltd).

Home range analysis

We explored whether overall home range size varied in relation to the proportion of habitats contained within it (10 habitat variables, see Table 1), several metrics of heterogeneity (mean patch size, number of habitat or Shanon index perform of patch size distribution) and individual-associated variables (body condition, sex and stopover duration). For this purpose, we performed General Linear Models (GLM) using the home range size (K50 and K95) as a response variable, while habitat cover and individual-associated variables were included as explanatory variables. According to the distribution of home range size (positive long tail distribution), we applied a negative binomial error distribution to the GLM in order to minimize issues related to the over-dispersion ratio in the models (i.e. as close as possible to 1; Zuur et al. 2009). Following a multi model inference (Burnham et al. 2011; Grueber et al. 2011), we generated a set of candidate models containing all possible variable combinations and ranked them by corrected Akaike information criterion (AICc) using the dredge function (R package MuMIn; Barton 2019). We only integrated the models complying with the following conditions: (i) models do not include simultaneously correlated covariates ($R^2 > 0.7$) and (ii) models do not include more than three variables to avoid over-parameterization due to the limited data set. Since the simultaneous inclusion of habitat cover and measures of habitat heterogeneity generated important multi-collinearity problems, we decided to perform two separate modelling: one with habitat cover within the home range and individual-associated variables; and a second one, with measures of habitat heterogeneity and individual-associated variables (results of this second modelling are shown in Appendix 5). We restricted this set of models using a cut-off of 2 AICc. The modelling with habitat cover resulted in 4 and 3 top models for K50 and K95, respectively (see Supplementary Material Ap. 5, Table A3). The modelling with measures of habitat heterogeneity resulted in 4 and 2 top models for K50 and K95, respectively (see Supplementary Material Ap. 5).

Following the same approach, we explored whether daily home range size (with a minimum of 10 positions) varied in relation to habitat cover within home range and individual-associated variables. According to the hierarchical structure of this data set (radio-tagged individuals survey each day), we treated the variable "individual identity" as a random effect, while considering the other explanatory variables (home range and individual-associated variables) as fixed effects (Zuur et al. 2009). Following a multi model inference using

General Linear Mixed Models with a negative binomial error distribution, the daily home range analyses resulted in a total of 2 and 3 top models for the K50 and K95, respectively (see Supplementary Material Ap. 5, Table A). We also used a secondary method based on PCA analysis detailed in Supplementary Material Ap. 6.

Roosting habitat selection

To provide information on roosting behaviour, we identified the habitats used between sunset and sunrise (roosting locations) and also estimated their distance to the daytime areas where birds were potentially foraging. We identified the habitat of all those locations on the vegetation map. We compared the proportions of roosting locations occurring in each habitat to identify the most used by *a posteriori* Wilcoxon test. For birds flying to a roosting location far away from the area used during daytime hours, we calculated the distance between the centroid of the home range exploited during daytime hours and the core of roosting locations. We then compared the proportions of habitats between these two areas (home range during daytime hours vs. roosting locations core) by *a posteriori* Wilcoxon test.

Diet of Bluethroat

To elucidate why birds tend to select specific habitats, we analysed their diet and the invertebrate availability. We collected 105 faecal samples during ringing operations for all sites in 2015 (n=52) and 2014 (n=30) and only in Urdains in 2012 (n=23). All remains identified in faeces were used to estimate the minimum number of prey items and the occurrence of each taxonomic group within each sample. While some bias in diet analyses was possible because small or soft-bodied preys are less easily detected, a strong correlation has been found between prey remains in droppings and the actual composition of the diet (Davies 1977a, 1977b). We also assessed prey biomass using predictive models based on the relationship between body length and mass of terrestrial arthropods (Hodar 1996; see Supplementary Material Ap. 7 for additional details). We explored which factors influenced prey abundance, testing explicitly the effects of age (young *vs* adult birds), sex and day using a Generalized Linear Model (GLM) with a Poisson error distribution. P-values were corrected for over-dispersion. Only taxa representing more than 2% of the prey abundance were considered

Invertebrate availability between habitats

We estimated the variation in the abundance of (near) ground invertebrates (the main feeding substrate of Bluethroats) between the two main habitats occupied by Bluethroats (corn crops and reedbeds). Given the large extension of the study area, we decided to focus our invertebrate sampling on three of the five trapping areas: the corn crop area, and Villefranque and Urdains reedbeds (Fig. A1). The corn crops in the other bank of the Nive River had similar management practices, so they are expected to have a similar invertebrate availability. We used 3 standardized coloured (yellow, white, blue) bowl traps and a pitfall glass per station (for a total of 12 stations, 6 in the corn crops, 3 in each reedbed). All stations were sampled simultaneously at 3 temporal stages in August 2015. Traps were deployed for four days. For more details, see Supplementary Material Ap. 8. For subsequent analyses, we pooled together the data of the three bowl traps of each station. We focused the analyses on those taxa whose remains had been found in faeces of trapped Bluethroats. We compared invertebrate availability, abundance and biomass between the two reedbeds and the corn crop using General Linear Models with a Poisson error distribution.

Unless specified, mean values are given ± se (standard error).

RESULTS

Stopover duration and body condition effect

Tagged Bluethroats stayed on average 5±1 (range 1-20) days upon capture in Barthes de la Nive, but showing a clearly non-Gaussian distribution where up to 13 individuals left the study area the next night after being captured (Fig. A3). The remaining 16 Bluethroats stayed on average 8.4 ± 1.3 days (see Table A1, Fig. A3).

Observed variation in stopover duration did not differ significantly between years (W=91, p=0.536), sites (Kruskal-Wallis H(3, 29) =1.11, p=0.774), sex (W=133, p=0.189), date of capture (r Spearman= -0.11, t_{27} = -0.59, p=0.558) or muscle development (r Spearman= -0.17, t_{27}= -0.92, p=0.365). The fat score was significantly associated with stopover duration (r Spearman= -0.40, t_{27}= -2.24, p=0.034). However, the individual trait that better explained stopover duration was fuel load, which was estimated from the residuals of body mass on body size (effects of body size on body mass: β=0.888, $F_{1,27}$=100.9, $p < 0.001$). Thus, Bluethroats with larger size-corrected fuel loads left the Nive basin earlier on average (r Spearman= -0.59, t_{27}= -3.78, $p< 0.001$; Fig. 1) than birds with smaller fuel stores. Additionally, we analysed whether stopover duration differed between habitats used. Irrespective of where they were trapped, birds that used corn crops remained significantly (W=23, $p<0.001$) longer (10 days ±1.1se, n=10) in the area than those not using this habitat type (2.7days ±0.6se, n=19; see Fig. 2).

Habitat selection

The 29 radiotracked juvenile Bluethroats provided 1718 positions during their stay. Bluethroat locations were not randomly distributed among habitats. Their distributions differed significantly from the theoretical null

distributions (Kolmogorov-Smirnov test D = 0.896, p <0.0001). The main habitats used by all birds were corn crops and reedbeds, either pure or mixed (Fig. 3). The distribution differed between birds staying one day, which preferred pure reedbed (W=55.5, p=0.034), and the remaining, which positively selected the corn crops (W=162, p=0.013). Birds stopping over for just one day made use of less habitat types (2.2± 0.3 [1-4] habitats) than birds staying longer (4.7± 0.5 [2-10]; W=180.5, p<0.001). However, during the first day of stay, there were no differences between them in the preferred habitat and number of them (tests Wilcoxon, p> 0.05, Fig.A4). Bluethroats positively selected pure and mixed reedbeds, corn crops and hydrophilous tall grasslands (Fig. 4). They moderately selected paths, wooded reedbeds and mesophic grasslands, while they avoided water, railways, ferns, wet grasslands, houses, woodlands and hay meadows.

Home range analysis

The average number of locations per individual was 59.2 ± 9 (22.5 ± 1.6 for birds staying one day, and 89 ± 12 for birds staying longer). The average overall K95 home range was 5.8 ± 1.8 ha with a large variation between individuals (range 0.016-46.5). The core area (i.e. K50) was on average 1.36 ± 0.35 ha (range 0.004-7.6). K95 areas were larger in birds staying more than one day (9.72 ± 3 ha) than in birds stopping over just one day (1.07 ± 0.46 ha; W = 23, p< 0.001). Similar results were obtained for the K50 core area: 0.28 ± 0.12 ha for long-staying birds, and 2.24± 0.53 ha for birds staying only 1 day (W = 18, p< 0.001).

Bluethroats with greater overall home range included more wet grassland, woodland and mesophilic grassland within their range, and also exhibited a longer stopover duration. On the other hand, Bluethroats with smaller overall home range exhibited larger quantities of body reserves and occupied areas with a higher proportion of reedbed (Table 2). Analyses performed for daily home ranges highlighted that Bluethroats with greater home range included more hay grasslands, open water, and woodlands; while Bluethroat with smaller daily home range occupied areas with a higher proportion of crop fields, natural paths and pure reedbeds (Table 2). In addition, analyses performed with measures of habitat heterogeneity, showed that Bluethroats with greater overall home range exhibited a more diversified home range (Appendix 5). According to AICc, measures of habitat heterogeneity performed better than habitat cover variables for K95, while it was the opposite for K50 (Appendix 5). A second analytical method based on PCA analysis gave similar results (see Supplementary Material Ap. 6).

Roosting habitat selection

We identified the overnight habitat (n= 103 nights) in 26 Bluethroats. Pure reedbed was the main roosting habitat, with 44.2% of the nights (Fig. 5). Mixed or wooded reedbeds were also well-represented within the roosting habitats, representing 17.5% and 16.8 %, respectively. So, reedbeds (pure, mixed and wood reedbed) were the preferred habitats for roosting (80.1± 8% of nights) in 23 birds that stayed for at least one night. Corn crops were also used by 5 birds but less frequently than reedbeds: 13.1 ± 6% of nights.

83% of the birds that spent the night in reedbeds (pure, mixed and wood reedbed) occupied the same reedbed during the day. This took place in 59 ± 9 % of the nights (Fig. 6). This particularly concerned the 13 Bluethroats which stopped over for just one day. Individuals staying for at least 2 days showed relatively predictable movements and selected repeatedly the same areas during the night. 27% of the birds (7) spent the night in a reedbed (Urdains or Villefranque) and normally moved during the day to a corn crop. This was noticed for 12.5 ± 5 % of the nights. We calculated the distance between roosting core areas and daytime (foraging) core areas. Birds flew on average 397 ± 33 m to reach its roosting location (n=10, range 80- 692 m). Five birds also used corn crops to stay during the night after using it also during the daytime (19 nights).

Diet analysis and habitat-specific invertebrate availability We obtained 105 faecal samples: 84 faecal samples from first year birds and 21 from adults, 55 from males and 47 from females. A total of 431 prey items were identified, 4.1 ± 0.8 on average per dropping. We found 14 orders of invertebrates (2.2 ± 0.3 on average per sample). The diet of Bluethroats was dominated by ants (Hymenoptera Formicidae), representing 45.5 % of prey items and occurring in 54% of the samples (Table 3). Spiders (Araneidae) were the second most abundant group (20.4%) with a similar occurrence to ants (53%); and beetles (Coleoptera) were the third most common group (10.2% of all prey items and 31% of the samples). These two last taxa were the main contributors to the consumed biomass, representing 64.7 % and 14.9%, respectively. We did not detect any significant effects of Bluethroat age and sex on prey abundance (Table 3). We did also observe that leafhoppers (Cicadellidae) were less consumed over time (Table 3).

Corn crops hosted significantly more invertebrates and biomass than reedbeds for beetles, flies(Diptera) and spiders in pitfalls, and for leafhoppers in bowls (Table 4). Corn crops also had higher availability of non-Formicidae hymenopterans than Urdains in bowls, but less than Villefranque. Finally, ants were more abundant in Urdains than in the other two sites.

DISCUSSION

Variation in stopover duration and home range size

Bluethroats showed large variation in their stopover duration and home range size in Barthes de la Nive. The observed mean differed from that obtained by Arizaga et al. (2013). Thus, stopover duration was shorter and home range larger in Barthes de la Nive (mean stopover duration of 5 days and mean home range size of 5.8 ha) than in Txingudi (9.6 days and 2 ha, respectively). Differences in stopover duration between these two sites were mediated by the fact that 45% of the radiotracked Bluethroats in Barthes de la Nive apparently departed the following night after capture, a circumstance that never took place in Txingudi (Fig. A3). If these short-staying individuals were excluded from the calculations, the stopover duration in Barthes de la Nive (i.e. 8.4 days) would conform better to the values obtained in Txingudi. After the signal of a bird disappeared from the place it was last detected, we carefully explored the whole study area by car the following day in its search, and sporadically during subsequent days. This makes us very confident that the stopover duration estimates obtained in Barthes de la Nive are reliable. Likewise, the fact that only one of the 29 radiotracked Bluethroats stayed longer than the life-expectancy of the transmitter would not alter these between-site differences or the general conclusions of our study (see below). The number of Bluethroats whose stay reached the expected functional life of the transmitters in Txingudi was slightly higher (3 out of 20) than in Barthes de la Nive, supporting the longer stopover duration of Bluethroats in the former site.

It could be argued that the higher number of short-staying Bluethroats in Barthes de la Nive was caused by the use of playbacks during the trapping sessions, which were not implemented in Txingudi. Although we cannot rule out completely this confounding factor as an alternative explanation to observed results, current evidence does not support this idea. Thus, the use of playbacks typically attracts Bluethroats with lower body reserves (Arizaga et al. 2015) and, as our results show, birds with less fuel loads would tend to have longer stopover durations (Alerstam and Lindström 1990; Salewski and Schaub 2007). This impact of playback on fuel loads of autumn migrating Bluethroats was consistent in the three wetlands on the Bay of Biscay (Gironde, Txingudi, Urdaibai) analysed by Arizaga et al. (2015) that are geographically very close to Barthes de la Nive. If Bluethroats do show transient vs. non-transient divergent behaviours during migration as have been described for other migratory species (Rappole and Warner 1976), playbacks might have also biased stopover duration estimates if they do preferentially attract transient individuals. However, a study of stopover duration using tape lures did not detect these transient Bluethroats during autumn migration (Arizaga et al. 2010). Likewise, neither the results obtained by Arizaga et al. (2015) would support this possibility, since playbacks do not seem to affect the number of Bluethroat recaptures, and this would be an expected outcome if playbacks promoted the capture of more transient individuals that would have less recapture prospects. Likewise, and contrary to what would be expected for their transient condition, these short-staying individuals did not move as much as would be expected after being trapped in Barthes de la Nive, and their first-day home range did not differ significantly from that observed for long-staying conspecifics.

Observed differences in stopover duration between Barthes de la Nive and Txingudi might explain the relatively low number of recaptures obtained in Barthes de la Nive when compared to Txingudi and also other nearby sites for which there is no radiotracking information so far (i.e. Gironde and Urdaibai; Arizaga et al. 2015). Additionally, these differences in recapture rates could be also promoted by the existence of overall home ranges that are nearly twice to three times larger in Barthes de la Nive than in Txingudi (Arizaga et al. 2013) and in Gironde (Musseau et al. 2017). These contrasting differences between Txingudi and Barthes de la Nive are potentially mediated by the strong differences in the degree of urbanization and habitat composition that seem to have profound consequences in the stopover behaviour of Bluethroats between two relatively close locations.

Habitat and roosting site selection

Migrating Bluethroats in Barthes de la Nive strongly selected reedbeds (pure and mixed) and other hydrophilic natural grasslands, which concurs with the favourite habitat that Arizaga et al. (2013) and Musseau et al. (2017) found for migrating and moulting conspecifics, respectively. Much less known was the preference of migrating Bluethroats for corn crops, although one study had detected this species in this crop type during migration (Gottschalk & Cover 2016) and some populations of Bluethroats seem to thrive and even breed successfully in some agricultural fields, such as oilseed rape crops (Cornulier et al. 1997; Berndt and Hölzel 2012, Chiron 2017). We did not find the preference of Bluethroats for tidal mudflats or low-halophytic vegetation described in other studies (Arizaga et al. 2013; Godet et al. 2015; Musseau et al 2017), but the representation of these habitats in Barthes de la Nive is relatively limited, which could explain this lack of use.

Our results showed that home-range size is smaller when birds occupied reedbeds (for overall home ranges) and corn crops (for daily home ranges). A potential explanation for this result is that these habitats might offer more trophic resources, which would prevent birds from making long foraging trips (Bibby and Green 1980; Chernetsov et al. 2004). Another complementary hypothesis for the higher occurrence of Bluethroats in these two habitat is that, given their dense structure, they could also provide a suitable shelter, not only for roosting during the night but also to rest during daytime between migration flight bouts. The use of reedbeds as roosting habitat has been described before in Bluethroats (Eybert et al. 2004; Harmange et al. 2016) and our study confirmed this preference and suggested that corn crops might occasionally play a similar role. In contrast, long-

staying Bluethroats seem to expand their home range probably because they are in high demand of food for refueling and, perhaps, because of the competition with conspecifics and other species (Chernetsov and Titov 2001; Fransson et al. 2008).
If home-range size is considered a proxy of habitat quality, inland reedbeds could be interpreted as a refuge or a more optimal habitat than corn crops, which might represent the most-commonly available substitution habitat (Godet et al. 2018), where birds needing to refuel would move due to competition and the limited availability of reedbeds.
In our site, Bluethroats encounter also some potentially unsuitable habitats such as woodlands, open water, mown grasslands and infrastructures (house, road, railway) that would explain why they had to fly away a relatively long distance from their preferred roosts (Harmange et al. 2016), expanding their home range size. Similar patterns have been shown in Briere for breeding Bluethroats (Godet et al. 2015).

We did not detect any difference between males and females in home range size, flight distance or stopover duration. Typically, small-sized, young and female Bluethroats are subordinated to large, adult and male conspecifics, respectively (Lindström et al. 1990, Moore et al. 2003). Our results suggest that Barthes de la Nive was occupied, not under an ideal despotic distribution, but under an ideal free distribution, where home range size would be determined by its habitat composition.

Diet of birds and invertebrate availability

The diet description for our study site fitted well with the trophic characterization made in other Bluethroat studies (Allano et al. 1998; Orłowski *et al.* 2014; Musseau et al. 2017). In decreasing order of importance, our study showed the relevance of ants (40.6% of prey; 8.7% of biomass), flies (resp. 14% and 6.5%), beetles (13.7%, 40%) and spiders (9.4%, 22.5%). Bluethroats typically forage on the ground (Orlowski et al. 2014, Allano et al. 1998, Cramp 1988) where ants are particularly abundant. As in other agricultural farms (Cornouiller et al. 1997), corn crops showed a relatively high insect abundance and biomass, which could explain why Bluethroats positively selected this habitat. Again and as a consequence of the relative scarcity of intertidal habitats, arthropods such as amphipods (Malacostraca Amphipoda) were absent from the diet of Bluethroat in Barthes de la Nive, although they have been found in other studies (Musseau et al. 2017; Allano et al. 1998).

Habitat management implications

Our study confirmed the importance of wetlands and their associated reedbeds in Barthes de la Nive for migrating Bluethroats, as it was also shown for other bird species stopping over in the region (Fontanilles et al. 2014). This reaffirms the need to conserve and potentially expand these valuable habitats, whose largest remnants in Southwestern France persist in the Nive/Adour river basin. These wetlands are mainly threatened by clogging and bush encroachment, particularly by invasive exotic tree species (i.e. *Acer negundo*, *Baccharis halimifolia*), so regular intervention is neededto maintain their characteristic aquatic vegetation.
Likewise, our results unexpectedly revealed a positive selection of corn crops by Bluethroats. The tall and dense arrangement of corn plants resemble the habitat structure of reedbeds. However, corn crops do not seem to constitute an ecological trap but a substitution habitat (Godet et al 2018), a human-induced opportunity for migrating birds. Anyway, further research would be required to further understand this selection process and whether it also takes place in other sites. Our preliminary results suggest that corn crops would provide plenty of food resources and a suitable shelter for birds stopping over in Barthes de la Nive. Our study using the Bluethroat as model species raises the question of how other bird species respond to the presence of corn crops during their stopovers. The corn crops of Barthes de la Nive are used by a large group of migratory species (Fontanilles not published), so that measures to maintain or increase the suitability of this common crop for birds around the limited wetland remnants should be encouraged. Among them, promoting organic farming and postponing the harvesting time after mid-October, when most insectivorous migrants are in or near their southern wintering quarters, would be relatively easy to implement and might have immediate payoff (Dänhardt et al. 2010).

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726 **cc**

727 **Table 1:** Abbreviations for the different habitats available in Barthes de la Nive with its corresponding
728 percentage of cover in the study area.

729

Code	Area (ha)	Habitats
WAT	32.91	open water
PRB	19.35	pure reedbed *Phragmites australis* > 75%
MRB	11.89	reedbed mixture *Phragmites australis* (>25%) + *Carex sp*
WOR	14.63	wooded reedbed (wood < 50%)
WGR	21.37	wet grassland
MGR	64.04	mown grassland
CGR	10.79	mesophilic grassland
CRO	69.4	crop field
FER	0.84	fern
TAL	3.79	hydrophilous tall herb
WOL	171.5	wood land
PAT	12.05	natural path
HOU	7.64	house
RAW	1.54	railway

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Table 2: Conditional average of estimates ($\beta_{cond.}$), adjusted SE ($SE_{adj.}$) and *P-value* for the variables included in the model set for daily and global home ranges (K50 & K95), (-) indicated a variable unselected. Abbreviations: crop field (CRO), mesophilic grassland (CGR), mown grassland (MGR), natural path (PAT), pure reedbed (PRB), open water (WAT), wet grassland (WGR), wood land (WOL), stopover duration (SOD), fuel loads (FUEL).

Home range	**50 % kernel**			**95% kernel**		
	$\beta_{cond.}$	$SE_{adj.}$	*P-value*	$\beta_{cond.}$	$SE_{adj.}$	*P-value*
Global home range						
CGR	0.485	0.151	0.001	-	-	-
PRB	-0.362	0.208	0.081	-0.876	0.250	<0.001
WGR	0.404	0.163	0.008	0.683	0.278	0.014
WOL	0.325	0.162	0.045	0.694	0.224	0.002
FUEL	-	-	-	-0.664	0.210	0.002
SOD	0.337	0.182	0.061	0.895	0.289	<0.001
Daily home range						
CRO	-	-	-	-1.532	0.278	<0.001
MGR	0.8355	0.2645	0.002	1.509	0.286	<0.001
PAT	-	-	-	-1.883	0.365	<0.001
PRB	-1.3473	0.3181	<0.001	-2.027	0.585	<0.001
WAT	0.6355	0.2279	0.005	-	-	-
WGR	-	-	-	0.683	0.269	0.014
WOL	0.6010	0.2229	0.007	-	-	-

Table 3: Percentage of each arthropod group in the faecal samples of 105 Bluethroats, occurrence frequency, proportion of total biomass and factors influencing the relative prey abundance (age: yearlings *vs* adults; sex and day). The number of prey items are given between brackets. "--" indicates no data available.

Order	Family	Abundance %	Occurrence %	Biomass %	Age effect		Sex effect		Day effect	
					z	p	z	p	z	p
Hymenoptera	Formicidae	45.48 (196)	54.29	8.34	0.998	0.318	-1.218	0.223	0.868	0.386
Arachnida Araneae	Araneidae	20.42 (88)	53.33	14.92	-0.986	0.324	0.373	0.709	-1.326	0.185
Coleoptera		10.21 (44)	31.43	64.70	-0.466	0.641	0.385	0.700	-0.614	0.539
Diptera		7.42 (36)	28.57	2.39	-0.010	0.992	0.462	0.644	0.281	0.779
Hymenoptera	non Formicidae	4.41 (19)	15.24	4.73	-0.193	0.847	0.803	0.422	-0.705	0.481
Hemiptera	Cicadellidae	3.25 (14)	13.33	2.45	-1.388	0.165	0.549	0.583	-1.993	**0.046**
Crustacea		3.32 (10)	9.52	2.48	0.008	0.993	-0.872	0.383	-0.772	0.440
Gastropoda		1.62 (7)	5.71	--						
Lepidoptera		1.62 (7)	6.67	--						
Neuroptera	Myrmeleontidae	1.16 (5)	3.81	--						
Arachnida Acarina		0.93 (4)	3.81	--						
Heteroptera		0.7 (3)	2.86	--						
Malacostraca Amphipoda		0.23 (1)	0.95	--						
Odonata		0.23 (1)	0.95	--						

Table 4: Abundance and biomass (mean ± SE) of the most consumed invertebrates by Bluethroats in corn crops (Crop), Villefranque reedbed (Rv) and Urdains reedbed (Ru), wchich were trapped in pitfall and coloured bowls. Numbers in bold indicate the site for which the abundance or biomass was significantly higher than one of the other sites (site shown after a slash symbol) or the other two sites. . Two hyphens represent no data available.

Order	Family	Trap	Abundance			Biomass (mg)		
			Crop	Ru	Rv	Crop	Ru	Rv
Hymenoptera	Formicidae	pitfall	0.2 ±0.1	**1.1 ±0.3**	0.2 ±0.1	0.04 ±0.02	**0.6 ±0.2 /Crop**	0.2 ±0.1
		bowl	0.3 ±0.1	--	0.6 ±0.2	0.03 ±0.02	0 ±0	0.2 ±0.1
Arachnida	Araneidae	pitfall	**3.5 ±1**	0.8 ±0.3	1.3 ±0.4	**7.5 ±2**	2.5 ±1	4.8 ±2.3
		bowl	1.9 ±0.4	1.2 ±0.5	2 ±0.6	3.4 ±0.8	5.9 ±2.9	**9.4 ±3.7**
Coleoptera		pitfall	**52.8 ±12.2**	0.1 ±0.1	2.1 ±0.5	**2006.9 ±449.1**	1.9 ±1.8	12.4 ±4.2
		bowl	**5.5 ±1.4**	0.7 ±0.3	**3.8 ±1.1**	**49.2 ±40.7**	0.9 ±0.6	8.2 ±3.7
Diptera		pitfall	**10.3 ±5.1**	0.3 ±0.2	1.1 ±0.3	**17.9 ±7.1**	0.8 ±0.8	1.1 ±0.5
		bowl	**24.5 ±6**	1.4 ±0.5	12.3 ±2.5	**42.2 ±8.8**	1.8 ±0.7	24.1 ±5
Hymenoptera	not Formicidae	pitfall	0.9 ±0.3	0.2 ±0.1	**1.4 ±0.5 /Ru**	0.7 ±0.3	0.1 ±0.1	**2.7 ±1.3**
		bowl	4.5 ±1	0.6 ±0.4	**8.9 ±1.6**	14.4 ±4.5	1.2 ±1.1	**43.6 ±8.2**
Hemiptera	Cicadellidae	pitfall	0.3 ±0.1	--	0.1 ±0.1	0.2 ±0.2	0 ±0	0 ±0
		bowl	**2.7 ±0.7**	0.1 ±0.1	0.7 ±0.3	**4 ±1.9 /Ru**	0 ±0	0.8 ±0.4

Fig. 1. Relationship between size-corrected fuel loads and stopover duration in Barthes de la Nive, n=29.

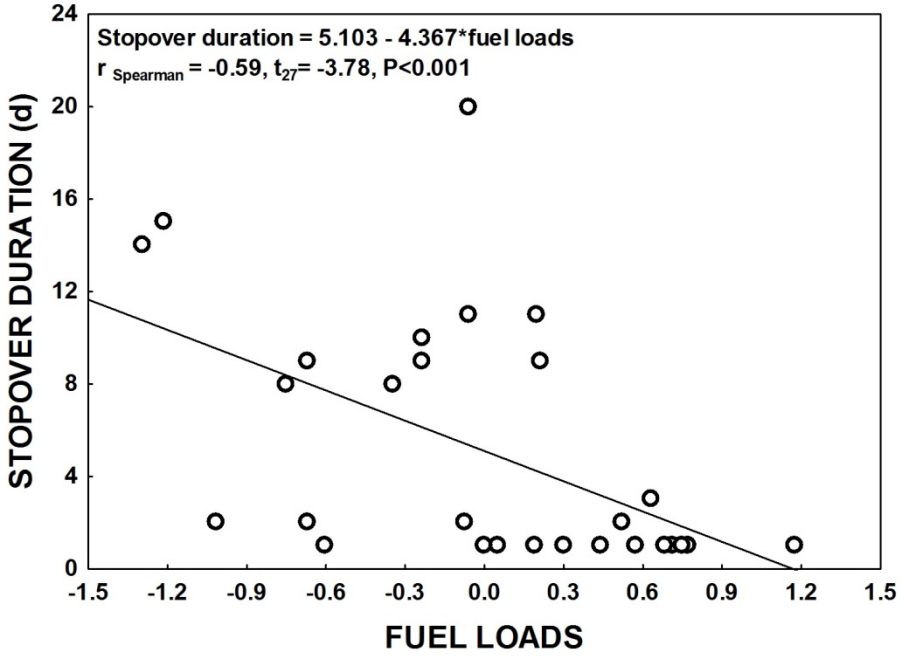


Fig. 2. Variation in stopover duration between bluethroats that used corn crops and birds that did not in Barthes de la Nive, mean ± SE.

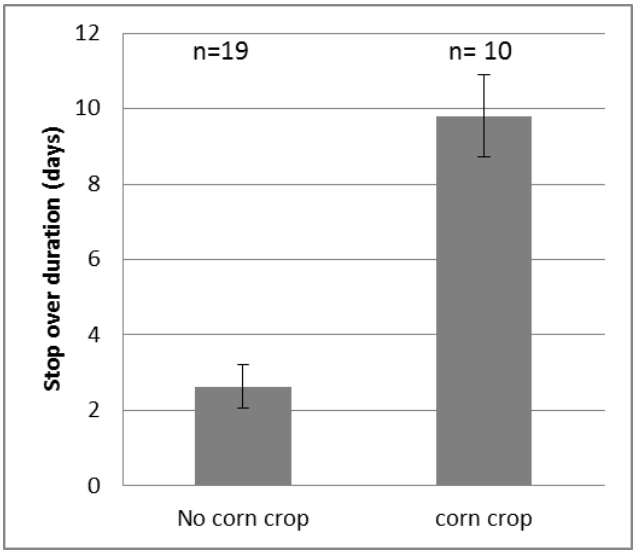


Fig. 3. Proportion (mean ± SE) of positions occurring in each habitat type of Barthes de la Nive for all Bluethroats, those staying one day and those staying more than one day. Abbreviations as in Table 1. The number of individual home ranges in which each habitat type was found is shown between brackets.

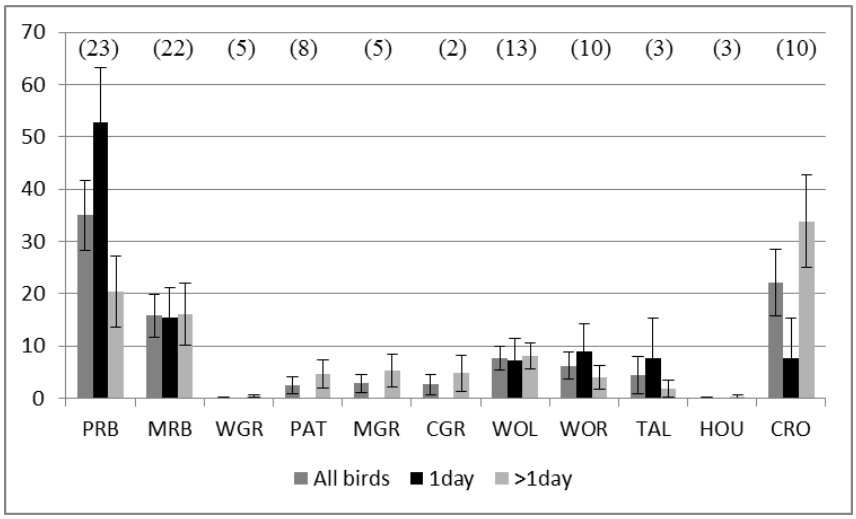
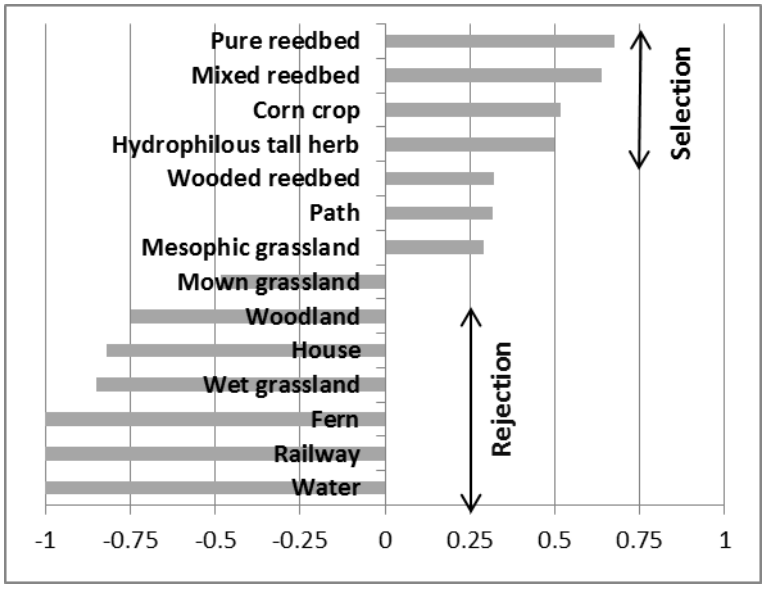


Fig. 4. Jacobs index values for each habitat in the Bluethroats radiotracked in Barthes de la Nive. Values below 0 represent habitat rejection, while values above 0 represent positive selection.



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